Five New Tribes in the Scrophulariaceae

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ABSTRACT. Four new tribes of Scrophulariaceae are described: Alonsoeae, Bowkerieae, Caprarieae, and Freylineae. The Globulariaceae are given new status as a tribe in the Scrophulariaceae. iridoids (Nicoletti et al., 1988). These compounds appear to mark a distinct clade within the Scrophulariales that also includes *Capraria* L. and the Pedaliaceae.

The relationships of many genera within the Scrophulariaceae are poorly understood. Thirty tribes are generally recognized, though some of these are clearly polymorphic and genera exist that do not fit within any recognized tribe. Recognition of the following tribes clarifies some of the relationships within the family.

Alonsoeae Barringer, tribus nov. TYPE: Alonsoa Ruiz & Pavón.

Herbae suffruticesve. Folia opposita vel verticillata. Inflorescentia centripeta, uniformis. Corolla explanato-rotata, resupinata, tubus nullus, labium posticum exterius. Stamina 4, antheris divaricatis vel in unam confluentes. Staminodia carentes. Capsula septicida, valvis integris bifidisve. Semina exarata.

While most species of Alonsoa are neotropical, Roux (1985) and Steiner (1989) have found South African plants that they refer to the genus. Similar plants were described by Kunze (1841) as Schistanthe Kunze, because they differed from Alonsoa in having the corolla slightly saccate, the two lowermost corolla lobes split to the base and the capsules ovate, obtuse, and emarginate (Hilliard & Burtt, 1984). They also differ in having eliaophores in the corolla sacs similar to those found in the South African Hemimerideae and the neotropical Angeloneae and Melospermeae. Whether the South African species are placed in Alonsoa or Schistanthe, they are closely related to the South American species (Steiner, 1989) and would also be placed in this tribe.

Herbs or subshrubs. Leaves opposite or whorled. Flowers in terminal racemes or panicles, resupinate; lower bracts leaflike, the upper reduced. Pedicels ebracteolate. Calyx 5-parted, the lobes imbricate. Corolla rotate, resupinate, the lower lobes (from resupination) outermost in bud. Stamens 4, anthers unithecate and reniform or bithecate and parallel to divaricate; staminodes lacking. Ovary biloculate, with many ovules; stigma subcapitate. Capsule septicidal, the valves entire or bifid. Seed with a solid, longitudinally furrowed coat.

A single genus native to Andean South America,

Bowkerieae Barringer, tribus nov. TYPE: Bowkeria Harvey.

Frutex arboresve. Folia opposita vel verticillata. Inflorescentia composita, pedunculis cymoso-multifloris rarius unifloris bibracteatis. Corolla tubo brevi. Stamina 4 vel 2, antherarum loculis apice confluentibus. Staminodia parva vel carentes. Capsula septicida, valvis integris bifidisve. Semina reticulata.

Shrubs or small trees. Leaves opposite or verticillate. Flowers in terminal or axillary cymes, sometimes forming panicles; not resupinate; bracts grading into leaves. Pedicels ebracteolate. Calyx 5-lobed, rarely 3-lobed, lobes imbricate or valvate. Corolla campanulate to funnelform with a conspicuous sac or pouch in the distal half of the tube, the upper lobes exterior in bud. Stamens 4 with 1 staminode occasionally present, or stamens 2 with 2 or 3 staminodes, anthers confluent, reniform. Ovary biloculate or rarely triloculate, with many ovules; stigma punctiform or slightly bifid. Capsule septicidal, the valves sometimes bifid. Seed with loose, thin reticulate coat.

Central America, and South Africa:

Alonsoa Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil.
150. 1798. TYPE: Alonsoa caulialata Ruiz
& Pavón fide Pennell (1920).

The true affinities of this tribe are difficult to discern. Bentham (1846) included it in the tribe Hemimerideae, but it is unlike any of the other genera in the tribe. Its often unithecate anthers, rotate corolla, and furrowed seeds are reminiscent of *Verbascum* L. It appears to be most closely related to *Verbascum* and *Scrophularia* L., which also have harpagioside and related 8β - 8α -methyl substituted

Three genera native to southern Africa:

Ixianthes Bentham, Companion Bot. Mag. 2: 54. 1835. TYPE: Ixianthes retzioides Bentham.

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Anastrabe E. Meyer ex Bentham, Companion Bot. Mag. 2: 54. 1835. TYPE: Anastrabe integerrima E. Meyer. Bowkeria Harvey, Thes. Cap. 1: 24, t. 37. 1859. TYPE: Bowkeria triphylla Harvey.

Bentham (1835, 1846) placed the genera in this tribe in the Cheloneae because of their cymose inflorescences. Within that tribe, he grouped it with African genera having inconspicuous staminodia or lacking them entirely. These genera are now segregated into the tribes Teedieae G. Don, Freylinieae Barringer, and Bowkerieae Barringer. The Bowkerieae differ from the Teedieae in having dehiscent capsules. They differ from the Freylineae in having a short corolla tube, valvate calyx, and confluent anthers. The seeds found in this tribe are similar to those of the Hemimerideae, but the Bowkerieae differ from that tribe in their shrubby habit, cymose inflorescences, and confluent anthers. Hilliard (1969) pointed out the close relationship between Anastrabe and Bowkeria. Ixianthes is a rare, monotypic genus of shrubs with whorled, linear leaves, 3- or 5-parted calyx, and flowers with two stamens. It differs from the other two genera in the tribe by having more elongate corollas, but it shares with the others the saccate corolla, shrubby habit, and confluent anthers that distinguish the tribe.

near Scoparia L. and Sibthorpia L., two other genera with actinomorphic corollas and alternate leaves. Bentham's Digitaleae, like his Cheloneae, was a grab bag of genera that are best arranged into different tribes (Thieret, 1967), with Capraria in a tribe of its own.

The genus is unusual in the family. The leaves are alternate and spiral, the corolla is campanulate and often radially symmetrical. The pollen is tricolpo-diorate, an unusual type in the family found only in Capraria L. and a few species of Mimulus L. (Niezgoda & Tomb, 1975). It is one of the few Scrophulariaceae containing harpagide compounds, iridoid glycosides found more commonly in Pedaliaceae but also found in Scrophularia L. and its relatives (Heinrich, 1989). Classification of the genus is still unsettled. It appears to have some relationship to the tribe Leucophylleae and the Myoporaceae (Niezgoda & Tomb, 1975).

Freylinieae Barringer, tribus nov. TYPE: Freylinia Pangella.

Frutices suffruticesve. Folia opposita vel verticillata rarissime alterna. Inflorescentia composita, pedunculis cymoso-multifloris rarius unifloris bibracteatis. Corolla tubo infundibuliformi, labium posticum exterius. Stamina 4, antherarum loculis distinctis. Staminodia parva vel carentes. Capsula septicida, valvis integris bifidisve. Semina reticulata.

Caprarieae Barringer, tribus nov. TYPE: Capraria L.

Herbae. Folia alterna. Inflorescentia centripeta. Corolla actinomorpha vel subzygomorpha campanulata lobis aequalibus. Stamina quinque vel quattuor aequales, antherarum loculis apice confluentis. Capsula loculicida. Semina reticulata.

Herbs. Leaves alternate. Flowers axillary or in terminal or axillary racemes. Bracteoles absent. Sepals 5, free or fused only at the base. Corolla actinomorphic or slightly zygomorphic, 5-lobed, broadly campanulate, not saccate or spurred, the lobes imbricate in bud, spreading. Stamens 5, inserted at the base of the corolla tube, the anthers exserted, bithecate, the thecae fused at the tip, divaricate. Stigma exserted, subcapitate to bilobed. Capsule loculicidal. Seed reticulate.

Shrubs or subshrubs. Leaves opposite or verticillate, rarely scattered along the stem. Flowers in terminal or axillary cymes, often secondarily clustered into panicles, bracts grading into leaves. Pedicels ebracteolate. Calyx 5-parted, lobes imbricate. Corolla tubular to funnelform, the upper lobes exterior in bud. Stamens 4, anthers with two parallel thecae. Staminodes short or absent. Stigma capitate, subcapitate, or sometimes slightly bifid. Capsule septicidal, secondarily loculicidal in Freylinia. Seed with thin reticulate exotesta.

Four genera native to southern Africa:

One genus native to Central America, western South America, and the Caribbean Islands, widespread as a weed in tropical regions:

Capraria L., Sp. Pl. 628. 1753. TYPE: Capraria biflora L.

Bentham (1876), Sprague (1921), and Thieret (1954) placed Capraria L. in the tribe Digitaleae

- Phygelius E. Meyer ex Bentham, Companion Bot. Mag. 2: 53. 1836. TYPE: Phygelius capensis E. Meyer ex Bentham.
- Freylinia Pangella ex Colla, Freyl. Gen. Add. Icon. (Hort. Ripul. 56). 1823. TYPE: Freylinia cestroides Colla.
- Antherothamnus N. E. Brown, Hooker's Icon. Pl. t. 3007. 1915. TYPE: Antherothamnus pearsonii N. E. Brown.
- Manuleopsis Thellung, Vierteljahr Nat. Ges. Zurich 60: 405. 1915. TYPE: Manuleopsis dinteri Thellung.

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This tribe is related to the Bowkerieae, described above, and is distinguished from that tribe by its anthers with two parallel thecae and its elongate corolla tube. Bentham (1876) described *Phygelius* as having confluent anthers but, as Dyer (1975) pointed out, the anthers have two parallel thecae.

Globularieae (A. DC.) Barringer, stat. nov. Globulariaceae A. DC. in Lamarck & A. DC., Fl. collections. I also thank the librarians at NY and MO for their help.

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Franç. 1805. TYPE: Globularia L.

Herbs or shrubs. Leaves alternate or rosulate. Flowers in globose capitula, terminal or rarely axillary; not resupinate; lower bracts not leaflike, forming an involucre. Calyx campanulate, 5-lobed, the lobes imbricate. Corolla tubular to funnelform, the upper lobes outermost in bud. Stamens 4 or rarely 2; staminodes lacking; anthers uniloculate, confluent. Ovary uniloculate, uniovulate; stigma subcapitate to minutely bifid. Fruit indehiscent. Seed with a solid, slightly reticulate coat.

Two genera native to the Mediterranean region of the Atlantic islands:

Globularia L., Sp. Pl. 95. 1754. TYPE: Globularia vulgaris L.
Poskea Vatke, Linnaea 43: 321. 1882. TYPE: Poskea africana Vatke.

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Many authors recognize this group as a distinct family following Wettstein (1891), while others combine it with the genera of the tribe Selaginieae and recognize that group as a family following Bentham (1876). Hallier (1903) was the first to combine these groups with the Scrophulariaceae. There is a very strong relationship among the tribes Manuleae, Selagineae, and Globularieae. They appear to form a distinct clade within the family that is characterized by a reduction in ovule and seed number and consolidation of the flowers into more densely packed inflorescences.

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